

# Natural enemies of the oil-collecting bee *Centris analis* (Fabricius, 1804) with notes on the behavior of the cleptoparasite *Coelioxys nigrofimbriata* Cockerell, 1919 (Hymenoptera, Apidae)

Daniele Regina Parizotto<sup>1</sup>

<sup>1</sup> Universidade Federal Rural de Pernambuco, Departamento de Agronomia, Programa de Pós-graduação em Entomologia Agrícola, Rua Manoel de Medeiros, s/n, Dois Irmãos, Recife, Brazil, 52171-900

Corresponding author: Daniele R. Parizotto ([dparizotto@gmail.com](mailto:dparizotto@gmail.com))

---

Academic editor: Michael Ohl | Received 11 January 2019 | Accepted 25 April 2019 | Published 28 June 2019

---

<http://zoobank.org/ACEC5BCD-AAAD-470D-8F1C-5E1B0F77E2E1>

---

**Citation:** Parizotto DR (2019) Natural enemies of the oil-collecting bee *Centris analis* (Fabricius, 1804) with notes on the behavior of the cleptoparasite *Coelioxys nigrofimbriata* Cockerell, 1919 (Hymenoptera, Apidae). Journal of Hymenoptera Research 70: 1–16. <https://doi.org/10.3897/jhr.70.33042>

---

## Abstract

This work presents a review of natural enemy species associated with *Centris analis* and summarizes the available information on life history, behavior, diversity, and specialization of these taxa. Records include over 20 species in ten genera from seven distinct families of Hymenoptera, Diptera and Coleoptera. These species are cleptoparasites or parasitoids of immature stages or adults. Some species seem to be occasional parasitoids, while others seem to be more frequent and responsible for significant mortality rates of immatures in nests. Three families of Hymenoptera represent the majority of natural enemy taxa found in *C. analis* nests: Apidae, Chrysididae, and Leucospidae. The most frequent parasitoid reared from nests was the wasp *Leucospis cayennensis* Westwood, followed by cleptoparasitic bee species of the genus *Coelioxys* Latreille. Vouchers of trap nest studies are identified for the first time and refer to *Coelioxys nigrofimbriata* Cockerell, which seems to have a strong association with nests of *C. analis*. Further direct observation notes about biology and behavior of *C. nigrofimbriata* are also provided.

## Keywords

Centridini, host, Neotropical region, nesting, parasite

## Introduction

*Centris analis* (Fabricius) is a solitary, oil-collecting bee with a broad geographic range that extends from central Mexico to southern Brazil (Moure and Melo 2012). It is often recorded in trap-nest surveys in various Brazilian biomes such as the Atlantic rainforest, caatinga, and cerrado (Jesus and Garófalo 2000; Aguiar and Martins 2002; Aguiar et al. 2005; Oliveira and Schlindwein 2009; Dórea et al. 2010; Rabelo et al. 2014; Moure-Oliveira et al. 2017). These bees are multivoltine, polylectic, and effective pollinators of native plants as well as crops (Dórea et al. 2010; Vilhena et al. 2012). These features led *C. analis* to be considered as a manageable pollinator in cultures such as acerola (*Malpighia emarginata*, Malpighiaceae), increasing orchard productivity and reducing pollination deficit (Oliveira and Schlindwein 2009; Magalhães and Freitas 2013). However, studies necessary to make its commercial use feasible are still lacking, including aspects of its life history, physiology, nesting preferences, population genetics, and natural enemies (Bosch and Kemp 2002; Oliveira and Schlindwein 2009; Alonso et al. 2012). This work aims to contribute an overview of the parasitoid and cleptoparasitic species known to attack *C. analis*, including data about distribution, biology and behavior of natural enemies, and direct observation notes on the behavior of the cleptoparasite *Coelioxys nigrofimbriata* attacking *C. analis* trap nests in Pernambuco, northeastern Brazil.

## Material and methods

### Field observations

Weekly observations of behavior of adults of *Coelioxys nigrofimbriata* were conducted on trap nests set up at commercial orchard Acerolândia, municipality of Paudalho, Pernambuco, Brazil, from November 2016 to December 2017. Two models of trap nests were used: compact and observation trap-nests. The compact nests were constructed with black cardboard with one end closed and inserted in wood blocks (modified from Garófalo et al. 1989). Each set contained 30 tubes, for a total of 240 cavities distributed in eight blocks. The observation trap nests consisted of linear cavities in wood blocks covered with a transparent plastic sheet fixed with a screw (modified from Cane 2004). Five sets were constructed with 30 tubes each, for a total of 150 cavities. The adult specimens that emerged from these nests were deposited in the entomological collection of the Department of Agronomy, Universidade Federal Rural de Pernambuco (CERPE), Recife, Brazil.

### Natural enemies of *Centris analis*

The many natural enemies of bees include parasites, commensals, predators, or scavengers of various organism groups including fungi, nematodes, mites and insects (Wcislo

and Cane 1996). There are only records of cleptoparasite or parasitoids species (ectoparasitoids of immature stages or endoparasitoids of adults) attacking *C. analis*. The cleptoparasite females lay eggs in nest cells, and their larvae consume both the host bee's food provision and the host egg or larva (Michener 2007; Groulx and Forrest 2018). Parasitoids lay eggs within or adjacent to bee larvae or eggs and their larvae develop and consume the bee larva or adult (Yeates and Greathead 1997).

## Results and discussion

The literature survey results indicate there are at least 22 species of natural enemies of *C. analis* in three orders of insects: Hymenoptera (3 families and 5 genera), Diptera (3 families and 3 genera) and Coleoptera (1 family and 2 genera) (Table 1). These species can produce 1 to 30% mortality rates in trap-nest studies and can be significant especially in aggregation nests (Aguiar and Martins 2002; Gazola and Garófalo 2003; Alonso et al. 2012). Besides parasitism, Jesus and Garófalo (2000) and Alonso et al. (2012) registered high mortality rates for immature *C. analis* in artificial trap-nests, with up to 60% due to unknown causes. A summary of general information and distribution records of natural enemies is presented below.

## APIDAE

### Ericrocidini

The tribe Ericrocidini includes 11 genera and 44 species, known only from the New World. All species of this tribe are cleptoparasites, most of them on *Centris* spp. (Rocha-Filho et al. 2009; Martins et al. 2017; Michener 2007), although *Mesoplia* Lepeletier also occurs in nests of *Epicharis* Klug (Rocha-Filho et al. 2008). Host associations are still poorly documented, sometimes only known from indirect observations (Michener 2007). Two species have been recorded in *C. analis* nests: *Aglaomelissa duckei* Snelling & Brooks, 1985 and *Mesocheira bicolor* Lepeletier & Serville, 1825.

*Aglaomelissa* Snelling and Brooks is a monotypic genus known from Costa Rica and northern South America (Michener 2007, Moure and Melo 2012). Rocha-Filho et al. (2009) reported that *A. duckei* emerged from nests of two species of *Centris* (*Heterocentris*) in the Brazilian Amazon: *Centris analis* and *C. terminata*. Considering the abundance and distribution of *C. analis*, *A. duckei* may be an important parasite in the Amazon region. However, because of the scarcity of information on *A. duckei* hosts, it is not possible to indicate how often this parasitic species attacks *C. analis*, or whether it is specific to *Centris* (*Heterocentris*).

*Mesocheira* Lepeletier and Serville is also a monotypic genus that occurs throughout the Neotropics, from Mexico to Paraguay. *Mesocheira bicolor* is frequently reported in trap nest studies but little is known about its cleptoparasitic behavior, biology and specificity. This species was recorded parasitizing both *Centris* (*Hemisiella*) and

*Centris* (*Heterocentris*) species, as follows: *C. dichrotricha* Moure, 1945, *C. nitida* Smith, 1874, *C. tarsata* Smith, 1874, *C. trigonoides* Lepeletier, 1841 and *C. analis* Fabricius, 1804 (Parker 1977; Morato et al. 1999; Jesus and Garófalo 2000; Aguiar and Martins 2002; Gazola and Garófalo 2002; Aguiar and Garófalo 2004; Aguiar et al. 2005). *Centris analis* is the only species of this list in subgenus *Centris* (*Heterocentris*), and the parasitism rates were low considering the wide distribution and the relative frequency of *M. bicolor* in trap-nesting bee studies. In observations performed in trap-nests set in the municipality of Paudalho, *Mesochora bicolor* females only attacked nests of *C. tarsata*, even though the abundance of *C. analis* nests was much higher in the studied area. Similar patterns were reported by Araújo et al. (2018) and Oliveira-Rebouças et al. (2018). The apparent preference of *M. bicolor* for *C. (Hemisiella)* nests may be due to the type of material used by female hosts to construct and/or provision the brood cells. The species of this subgenus are known to use a mixture of sand and oils (Vinson et al. 1996; Morato et al. 1999; Pereira et al. 1999) while *C. (Heterocentris)* females tend to use plant material and oils (Jesus and Garófalo 2000; Aguiar and Garófalo 2004; Oliveira and Schlindwein 2009). The low rates of parasitism could also be due to the differences in larval foods stored in brood cells. The cell provisions of *C. analis* consist of pollen and nectar without floral oils, which may be a characteristic of the subgenus (Jesus and Garófalo 2000; Aguiar and Garófalo 2004), while *C. tarsata* females use a mixture of pollen, nectar, and oil (Aguiar and Garófalo 2004). Based on the available information, it seems *M. bicolor* is not an effective parasite of *C. analis*, with only occasional occurrence in nests of this species.

## Megachilini

The tribe Megachilini includes a large number of taxa with great morphological and behavioral diversity. Most of the cleptoparasitic species belong to the cosmopolitan genus *Coelioxys*, which includes over 200 species in South America (Moure et al. 2012, Michener 2007). Most *Coelioxys* spp. are cleptoparasites of *Megachile*, although there are records of parasitism of other genera of both Megachilinae and Apinae, including *Centris* (Rocha-Filho and Packer 2015; Michener 2007).

*Coelioxys* spp. have often been recorded as parasites of *C. analis* in samples with trap nests (Table 1). In most of these studies, one single species of *Coelioxys* was observed parasitizing *C. analis* nests, but in several of them the species is not identified due to the lack of taxonomic studies of the genus (Rocha-Filho 2015). The present work reports on vouchers identified to species level for the first time. All specimens examined belonged to *Coelioxys nigrofimbriata* (see references in Table 1). Only Aguiar and Martins (2002) and Gazola and Garófalo (2009) found more than one *Coelioxys* species attacking *C. analis* nests in the same area; two and three, respectively. The material from Gazola and Garófalo (2009) identified as *Coelioxys* aff. *uhleri* from Estação Ecológica de Paulo de Faria actually corresponds to *C. nigrofimbriata*. The other two species reported by Gazola and Garófalo (2009), the material of Aguiar and Martins

**Table 1.** Summary of records of *Centris analis* natural enemies.

Taxa	Locality	References
<b>HYMENOPTERA</b>		
<b>APIDAE</b>		
Ericrocidini		
<i>Aglaomelissa duckei</i>	BRAZIL: Acre	Rocha-Filho et al. 2009
<i>Mesocheira bicolor</i>	BRAZIL: São Paulo	Jesus and Garófalo 2000; Gazola and Garófalo 2002; Couto and Camillo 2007
Megachilini		
<i>Coelioxys nigrofimbriata</i>	BRAZIL: Pernambuco, BRAZIL: São Paulo	This study Jesus and Garófalo 2000; Gazola and Garófalo 2002; Couto and Camillo 2007; Gazola and Garófalo 2009
<i>Coelioxys</i> spp.	BRAZIL: Minas Gerais BRAZIL: Paraíba BRAZIL:Paraná BRAZIL: São Paulo	Araújo et al. 2018 Aguiar and Martins 2002 Oliveira and Gonçalves 2017 Gazola and Garófalo 2009; Araújo et al. 2018;
<b>CHRYSIDIDAE</b>		
Chrysidini		
<i>Chrysis</i> sp.	BRAZIL: Paraná	Oliveira and Gonçalves 2017
<b>LEUCOSPIDAE</b>		
<i>Leucospis bulbiventris</i>	COSTA RICA: Guanacaste	Cooperband et al. 1999
<i>Leucospis cayennensis</i>	COSTA RICA: Guanacaste BRAZIL: São Paulo	Cooperband et al. 1999 Jesus and Garófalo 2000; Gazola and Garófalo 2002, 2003, 2009; Couto and Camillo 2007; Alonso et al. 2012; Moure-Oliveira et al. 2017
<i>Leucospis</i> spp.	BRAZIL: Paraná BRAZIL: São Paulo BRAZIL: Bahia	Oliveira and Gonçalves 2017 Gazola and Garófalo 2009 Oliveira-Rebouças et al. 2018
<b>DIPTERA</b>		
<b>BOMBYLIIDAE</b>		
Anthracini		
<i>Anthrax oedipus</i>	BRAZIL: São Paulo	Rocha-Filho et al. 2017 Gazola and Garófalo 2009
<i>Anthrax macquarti</i>	BRAZIL: São Paulo	Gazola and Garófalo 2009; Moure-Oliveira et al. 2017; Araújo et al. 2018
<i>Anthrax</i> spp.	BRAZIL: Minas Gerais	Araújo et al. 2018
<b>CONOPIDAE</b>		
Conopini		
<i>Physocephala aurifrons</i>	BRAZIL: São Paulo	Santos et al. 2008; Couto and Camillo 2014
<i>Physocephala benneti</i>	BRAZIL: São Paulo	Santos et al. 2008; Couto and Camillo 2014
<i>Physocephala bipunctata</i>	BRAZIL: São Paulo	Couto and Camillo 2014
<i>Physocephala cayennensis</i>	BRAZIL: São Paulo	Santos et al. 2008; Couto and Camillo 2014
<i>Physocephala inhabilis</i>	BRAZIL: São Paulo	Couto and Camillo 2014
<i>Physocephala rufithorax</i>	BRAZIL: São Paulo	Santos et al. 2008; Couto and Camillo 2014
<i>Physocephala soror</i>	BRAZIL: São Paulo	Santos et al. 2008
<i>Physocephala spheniformis</i>	BRAZIL: São Paulo	Santos et al. 2008; Couto and Camillo 2014
<i>Physocephala</i> sp.	BRAZIL: São Paulo	Santos et al. 2008
<b>PHORIDAE</b>		
<i>Melaloncha</i> sp.	São Paulo: BRAZIL	Ament et al. 2014
<b>COLEOPTERA</b>		
<b>MELOIDAE</b>		
Nemognathini		
<i>Nemognatha</i> sp.	São Paulo: BRAZIL	Gazola and Garófalo 2009
Tetraonycini		
<i>Tetraonyx</i> sp.	Amazonas: BRAZIL	Morato et al. 1999



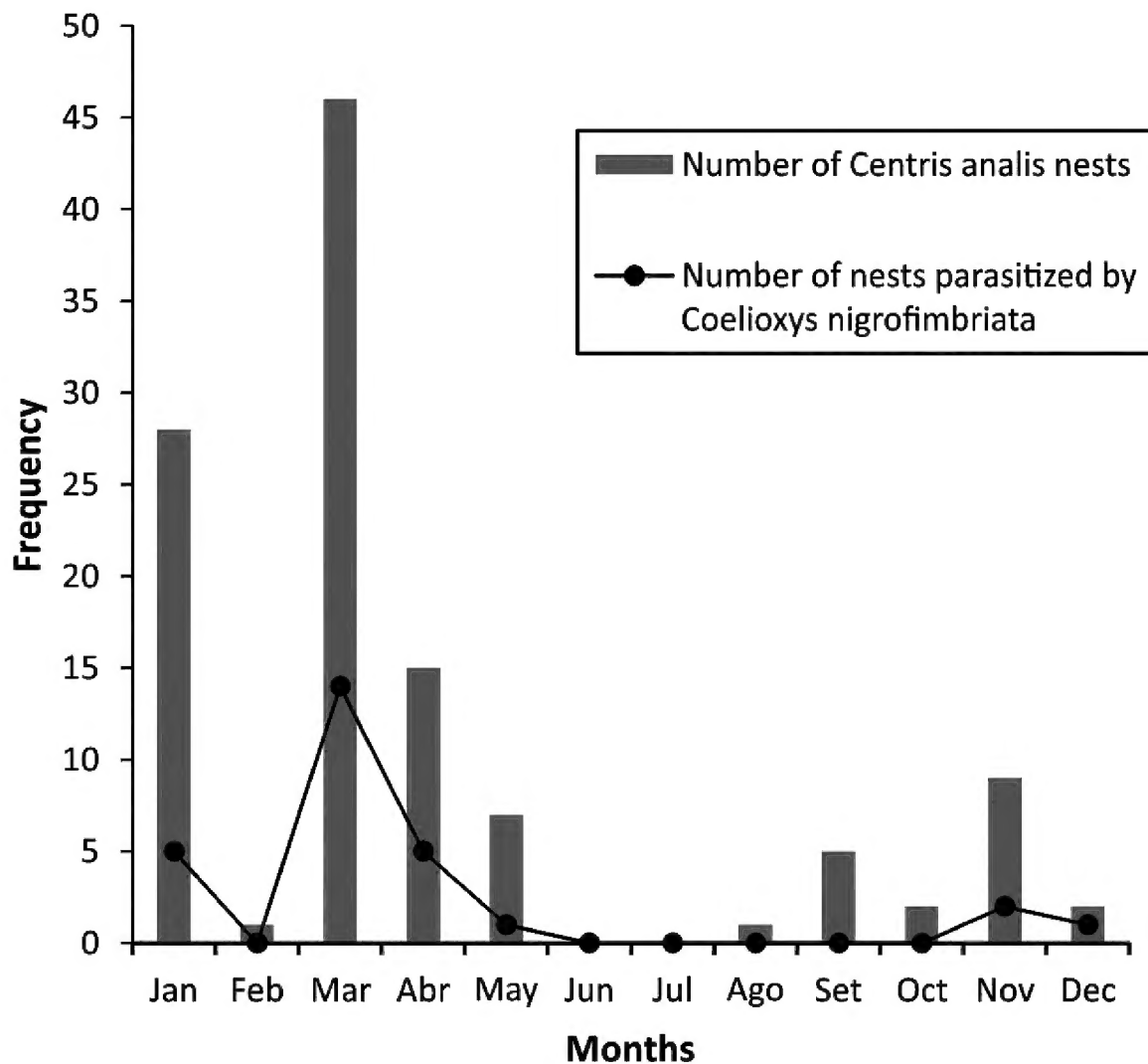
(2002) and also the other surveys listed in Table 1 as *Coelioxys* spp. could not be examined to confirm the identification at this time.

**Behavior of *Coelioxys nigrofimbriata*.** This species was described from the state of Amazonas, Brazil, but the observation of specimens in trap-nest studies demonstrated that it is widely distributed in Brazil, occurring from Amazonas to Paraná. *Coelioxys nigrofimbriata* females usually hover in front of the trap nests to locate a nest that is being provisioned. Often, only one or two females of the cleptoparasite bee were seen at the same time in the wooden blocks. The parasite enters, inspects and deposits an egg when the host female is absent. When the amount of larval food is not sufficient, the parasite leaves the nest, lands near the nest entrance and waits for the host to deposit more pollen (up 70 min, according to Gazola and Garófalo 2002). This behavior of ovipositing into open cells, and waiting near the entrance agrees with the general patterns described for the genus (Scott et al. 2000, Michener 2007, Vinson et al. 2011). The females of *C. nigrofimbriata* were observed within 3 to 20 cm of the nest, with the head directed towards the nest entrance, similar to what was described for *Coelioxys chichimeca* Cresson, 1878 (Vinson et al. 2011). Females of *C. analis* that returned from foraging trips expelled parasites that were close to their nests. However, the parasites would return a few minutes later and repeat the behavior. The observations described here agree with the remarks made by Gazola and Garófalo (2002) (cited as *Coelioxys* sp.).

*Centris analis* was active throughout the year, with nest construction recorded in every month except June and July, while the *C. nigrofimbriata* attacks occurred between November and May. *Centris analis* built 116 nests during the study period, of which 28 were attacked by *C. nigrofimbriata*. Of the 116 nests, 97 were built during the hot and wet season, with the highest frequency occurring in March (n=46). These nests produced 274 individuals of the host species and 32 *C. nigrofimbriata*. The number of brood cells constructed by *C. analis* per nest ranged from one (n= 19) to nine cells (n= 1), with four (n=22) and five (n= 22) cells being the most abundant. Of the 28 nests attacked by cleptoparasite bees, 24 produced only one parasite, and four produced two parasites. The highest frequencies of attacks occurred in the months that *C. analis* had the highest nesting frequencies (January, March and April) (Figure 1). *Coelioxys nigrofimbriata* parasitized exclusively nests of *C. analis* even though there were also nests of *C. tarsata* in the same area. These data demonstrated that parasitism activities of *C. nigrofimbriata* were strongly synchronized and dependent on the construction of nests by *C. analis*.

## CHRYSIDIDAE

Chrysididae is a diverse and cosmopolitan family that includes about 3000 species in 80 genera. The biology of chrysidids is still poorly known, with few studies about their hosts (Tormos et al. 1996). The group is classified in four subfamilies known for attacking Phasmatodea as well as other Hymenoptera such as Diprionidae, Tenthredinidae, bees and solitary wasps (Soon and Sarma 2011; Melo et al. 2012). Most species of the subfamily Chrysidinae are parasites of bee and wasp larvae or are cleptoparasites



**Figure 1.** Number of *Centris analis* nests built and number of nests attacked by *Coelioxys nigrofimbriata* from January to December 2017.

of larval provisions of their hosts (Morgan 1984; Melo et al. 2012). Most hosts are solitary wasps that build mud-pot nests or that use preexisting cavities in soil or wood, such as Vespidae, Sphecidae, Crabronidae, and Megachilinae (Pärn et al. 2015; Kimsey 2006; Torretta 2015). The genus *Chrysis* L. is largest genus of the group, but there is little information about their host species. Species of *Chrysis* are known to have various levels of host specialization (Pärn et al. 2015). The only record of a *Chrysis* species parasitizing a nest of *C. analis* was recently published by Oliveira and Gonçalves (2017) in southern Brazil. The data indicates that this species is a non-specific parasite in *C. analis* nests, as these authors also recorded the same species of *Chrysis* attacking nests of *Megachile susurrans* Haliday, 1836 and three species of Vespidae – *Monobia angulosa* Saussure, 1852, *Pachodynerus guadulpensis* (Saussure, 1853) and *Pachodynerus grandis* Willink & Roig-Alsina, 1998.

## LEUCOSPIDAE

This family of chalcidoid parasitoids includes four genera and about 141 species distributed worldwide (Lima and Dias 2018; Melo et al. 2012; Noyes 2017), most of them in the genus *Leucospis* Fabricius, with approximately 120 described species

and 45 known to occur in the Neotropical Region (Noyes 2017). These wasps are larval parasitoids of solitary bees (Apidae and Megachilidae) and less frequently aculeate wasps (Sphecidae and Vespidae) (Torreta et al. 2017). Females usually use their ovipositor to drill through the cell walls of the host nest and the immature develops as an ectoparasite feeding on the fluids of the host larva. Hosts are known only for about 30 species (Grissell and Cameron 2002), four of which were reported from nests of *C. analis*: *Leucospis bulbiventris*, *L. cayennensis*, *L. manaica*, and *L. sp.* (Table 1). Among these species, *L. cayennensis* is the most common natural enemy of *C. analis* (Boucek 1974; Gazola and Garófalo 2003). This species also was reported in nests of *Centris tarsata* Smith, 1874 (Chandler et al. 1985), *Centris bicornuta* Mocsáry, 1899, *Centris nitida* Smith, 1874, *Centris vittata* Lepeletier, 1841 (Cooperband et al. 1999), *Centris labrosa* Friese, 1899 (Gazola and Garófalo 2003), *Tetrapedia diversipes* Klug, 1810 (Camillo 2000) and *Tetrapedia curvitaris* Friese, 1899 (Gazola and Garófalo 2003).

*Leucospis cayennensis* is widely distributed from Mexico to Argentina. However, the frequency of attacks on nests of *C. analis* is not homogeneous throughout this distribution. This species was associated with nests of *C. analis* only in Costa Rica and the states of Paraná and São Paulo in Brazil (Table 1). The highest rates were observed in studies conducted in São Paulo (Gazola and Garófalo 2002, 2003), with 25% of cell parasitism by *L. cayennensis*. This variation, in addition to the records of *L. cayennensis* in nests of many others species (Torreta et al. 2017), suggests that this wasp is not specific to *C. analis*. However, *Leucospis cayennensis* may still have an important role as natural enemy of *C. analis* in aggregations of trap-nests due to their behavior. Gazola and Garófalo (2003) reported that the parasitoid females may repeatedly return to the nesting area for several days and that a single female can attack up to 24 nests. More details about the biology of this species can be found in Gazola and Garófalo (2002, 2003).

## DIPTERA

### BOMBYLIIDAE

Bombyliidae is one of the largest families of true flies with over 5000 described species. Their representatives are most abundant and diverse in arid and semiarid regions of the world, with about 450 species in the Neotropical Region (Ávalos-Hernández et al. 2014; Yeates and Greathead 1997; Carvalho et al. 2012). *Anthrax* Scopoli is also a diverse taxon, with 248 species worldwide, whose immature stages are all ectoparasitoids of larvae and pupae of holometabolous insects living in tubular nests or cells (Marston 1970, Ávalos-Hernández et al. 2014). Yeates and Greathead (1997) listed 70 species as ectoparasitoids of larvae and pupae of bees and wasps, and over 300 host records, but available information about host preferences and specificity for the genus is still scarce (Marston 1970). Among the bees, six studies recorded three species of



*Anthrax* in nests of *C. analis* (Table 1). In all these trap-nest studies, *Anthrax* species seemed to be generalist, emerging from nests of *C. analis* as well as other species of bees and wasps. No additional data was found on the parasitic behavior of *Anthrax* in nests of *C. analis*.

## CONOPIDAE

Conopidae is a widespread family of flies with about 780 species and 56 genera (Carvalho et al. 2012). The larvae of species for which biology is known are obligatory endoparasitoids of other insects. Representatives of three subfamilies (Conopinae, Myopinae and Dalmanniinae) are known as internal parasites of aculeate Hymenoptera, and some species may have a negative effect on populations of pollinators (Gibson et al. 2013; Melo et al. 2008). Females attack adult bees, inserting an egg on or within the bee's abdomen while they are foraging, or in flight. The larva develops inside the abdomen of the host, feeding on internal tissue and hemolymph, and pupates in situ, killing the host (Santos et al. 2008).

Species of the genus *Physocephala* Schiner are solitary koinobiont endoparasitoids of several genera of bees such as *Anthidium* Fabricius, *Anthophora* Latreille, *Apis* Linnaeus, *Bombus* Latreille, *Centris* Fabricius, *Epicharis* Klug, *Eulaema* Lepeletier, *Euglossa* Latreille, *Halictus* Latreille, *Megachile* Latreille, and *Xylocopa* Latreille (Rasmussen and Cameron 2004; Melo et al. 2008; Santos et al. 2008; Couto and Camillo 2014). Santos et al. (2008) reported on conopid flies attacking *C. analis* and recorded nine species of *Physocephala* in southeastern Brazil (Table 1). Couto and Camillo (2014) also recorded eight *Physocephala* species emerging from dead specimens of *C. analis*. Couto and Camillo (2014) also observed that parasitized females present behavioral changes, and deposited extra oil on the nest occlusion or closed empty nests. These parasitic associations do not appear to be specific, but impact the behavior of the female bees. Behavior data for *C. analis* are still scarce, but these parasitic flies can have a high incidence of attacks and decrease bee populations as reported for *Bombus* spp. by Abdalla et al. (2014) and Malfi et al. (2014).

## PHORIDAE

Phoridae is a cosmopolitan family of flies with over 4000 described species (Brown and Smith 2010). Many species are well known as parasitoids of corbiculate bees such as stingless bees, bumblebees and honey bees (Lucia et al. 2013; Ament et al. 2014). There are also records of species of *Melaloncha* Brues attacking Augochlorini (Halictidae) (Wcislo et al. 2004), Centridini (Apidae) and Euglossini (Apidae) species (Ament et al. 2014). The genus occurs only in the Neotropical Region and comprises the largest group of bee-killing parasitoids, with 167 described species. Female flies attack bees

by injecting an egg into their body through the membrane between sclerites and the larvae develop as internal parasitoids, consuming and killing the hosts (Brown 2004; Brown and Smith 2010; Brown 2016). The record is exceptional and it is based on the observation of a puparium removed from the mesosoma of a *Centris analis* (Ament et al. 2014).

## COLEOPTERA

### MELOIDAE

Meloidae is a family of beetles that includes almost 2500 species in approximately 120 genera. Meloid larvae are known as parasites of grasshoppers and larvae of Apoidea or other aculeate Hymenoptera (Bologna and Pinto 2001; Lückmann and Assmann 2006). The family has a distinctive form of metamorphosis, with the presence of a triungulin first instar in most taxa. This first instar, depending on the group, feeds on eggs of Acridoidea or provisions and larvae of Apoidea or other aculeate Hymenoptera. In the taxa that attack apoid hosts, the triungulin is phoretic, and is taken to the larval food indirectly by the adult bees that visit flowers (Bologna and Pinto; 2001). Some species have been documented as parasites of *Melitoma* Lepeletier and Serville (Roubik 1989), *Epicharis* Klug (Gaglianone 2005), *Monoeca* Lepeletier and Serville (Rozen et al. 2006) and *Eufriesea* Cockerell (Kamke et al. 2008). *Tetraonyx* Latreille (Morato et al. 1999) and *Nemognatha* Illiger (Gazola and Garófalo 2009) were recorded in *C. analis* nests trap-nest surveys, but without species-level identification, information about the biology or parasitic behavior.

## Conclusion

Although there are many studies about the life history of *C. analis* (see Jesus and Garófalo 2000; Alonso et al. 2012; Couto and Camillo 2014), much still needs to be described, especially regarding interactions with natural enemies. With the exception of the detailed observations made by Gazola and Garófalo (2003) about *L. cayennensis*, little is known about behavioral strategies of species attacking *C. analis*. Most records are scattered, and lack information about biology and parasitism rates (Wcislo and Cane 1996). Aspects such as parasite-host synchronicity and the effects of the presence of multiple natural enemies on the same populations of *C. analis* need to be better investigated. In addition, up to 70% of the mortality rates in immature stages of the trap nests are due to unknown causes (Oliveira and Schlindwein 2009; Alonso et al. 2012). Bacteria, fungi, mites and viruses may be responsible for part of this mortality in *C. analis*, but are still unknown. Pathogenic fungi, for example, are known to cause diseases in solitary bees (*Megachile rotundata* and *Osmia* spp.) leading to high levels of mortality in managed populations (Bosch and Kemp 2002).

The present work aimed to summarize available information on natural enemies and contribute to the taxonomic identification of the *Coelioxys* spp. that attack *C. analis* (Table 1). The new data about distribution, biology and behavior of *Coelioxys nigrofimbriata* provide a new perspective on the intricate relationships between host and cleptoparasitic bees. The other species of natural enemies of *C. analis* listed here do not seem to have this strong association. However, some of them can also reach high parasitism rates, such as *Leucospis cayennensis*. Therefore advanced studies about natural enemies of *Centris analis* are necessary to make commercial rearing feasible. As pointed out by Bosch and Kemp (2002) the mortality levels often decrease as knowledge on the developmental biology of the pollinator increases, and rearing methods are improved.

## Acknowledgments

The author would like to thank Nadia Carneiro Lacerda for allowing the field observations on private property, and Léo Correa da Rocha-Filho for the identification of *Coelioxys nigrofimbriata*, comments and suggestions on a previous version of this paper. I also thank the Laboratório de Escrita Científica (Ana Dal Molin and Karin Fehlauer-Ale) for the help with the English version of this manuscript. This study was supported by CNPq (Process DCR– 300501/2016–1) and FACEPE (APQ, Process DCR–0013–5.01/16).

## References

- Abdalla FC, Sampaio G, Pedrosa M, Sipriano TP, Domingues CEC, Silva-Zacarin ECM, Camargo DA (2014) Larval development of *Physocephala* (Diptera, Conopidae) in the bumble bee *Bombus morio* (Hymenoptera, Apidae). *Revista Brasileira de Entomologia* 58: 343–348. <https://doi.org/10.1590/S0085-56262014000400003>
- Aguiar AJC, Martins CF (2002) Abelhas e vespas solitárias em ninhos-armadilha na Reserva Biológica Guaribas (Mamanguape, Paraíba, Brasil). *Revista Brasileira de Zoologia* 19: 101–116. <https://doi.org/10.1590/S0101-81752002000500005>
- Aguiar CML, Garófalo CA (2004) Nesting biology of *Centris (Hemisiella) tarsata* Smith (Hymenoptera, Apidae, Centridini). *Revista Brasileira de Zoologia* 21: 477–486. <https://doi.org/10.1590/S0101-81752004000300009>
- Aguiar CML, Garófalo CA, Almeida GF (2005) Trap-nesting bees (Hymenoptera, Apoidea) in areas of dry semideciduous forest and caatinga, Bahia, Brazil. *Revista Brasileira de Zoologia* 22: 1030–1038. <https://doi.org/10.1590/S0101-81752005000400031>
- Alonso J, Silva J, Garófalo C (2012) The effects of cavity length on nest size, sex ratio and mortality of *Centris (Heterocentris) analis* (Hymenoptera, Apidae, Centridini). *Apidologie* 43: 436–448. <https://doi.org/10.1007/s13592-011-0110-0>

- Ament D, Freiria G, Rocha-Filho LC, Lama M, Garófalo CA (2014) A scientific note on the first records of *Melaloncha* Brues, 1904 (Diptera: Phoridae) parasitizing Euglossini and Centridini bees. *Apidologie* 45: 266–268. <https://doi.org/10.1007/s13592-013-0246-1>
- Araújo GJ, Fagundes R, Antonini Y (2018) Trap-nesting Hymenoptera and their network with parasites in recovered riparian Forests Brazil. *Neotropical Entomology* 47: 26–36. <https://doi.org/10.1007/s13744-017-0504-4>
- Ávalos-Hernández O, Kits J, Trujano-Ortega M, García-Vázquez UO, Cano-Santana Z (2014) New records of bee flies (Diptera, Bombyliidae) from Cuatro Ciénegas, Coahuila, Mexico. *ZooKeys* 422: 49–85. <https://doi.org/10.3897/zookeys.422.7598>
- Bologna MA, Pinto JD (2001) Phylogenetic studies of Meloidae (Coleoptera), with emphasis on the evolution of phoresy. *Syst Entomol* 26: 33–72. <https://doi.org/10.1046/j.1365-3113.2001.00132.x>
- Bosch J, Kemp WP (2002) Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bulletin of Entomological Research* 92: 3–16.
- Boucek Z (1974) A revision of the Leucospidae of the World. *Bulletin of the British Museum (Natural History), Entomology, Supplement* 23: 1–24.
- Brown B (2016) Two new bee-killing flies from Brazil (Insecta: Diptera: Phoridae: *Melaloncha*). *Biodiversity Data Journal* 4: e7715. <https://doi.org/10.3897/BDJ.4.e7715>
- Brown BV, Smith PT (2010) The bee-killing flies, genus *Melaloncha* Brues (Diptera: Phoridae): a combined molecular and morphological phylogeny. *Systematic Entomology* 35: 649–657. <https://doi.org/10.1111/j.1365-3113.2010.00540.x>
- Brown BV (2004) Revision of the subgenus *Udamochiras* of *Melaloncha* bee-killing flies (Diptera: Phoridae: Metopininae). *Zoological Journal of Linnean Society, London* 140: 1–42. <https://doi.org/10.1111/j.1096-3642.2004.00086.x>
- Camillo E (2000) Biologia de quatro espécies de Tetrapedia em ninhos armadilha (Hymenoptera, Apidae, Tetrapediini). PHD Thesis, Universidade de São Paulo.
- Cane JH (2004) Exposing their progeny: using X-rays and observation nests to study and manipulate cavity-nesting bees. In *Proceedings of the 8<sup>th</sup> IBRA International Conference on Tropical Bees and VI Encontro sobre Abelhas*. Ribeirão Preto, SP, 99–100.
- Carvalho CJB, Rafael JAR, Couri MS, Silva VC (2012). Diptera. In: Rafael J, Melo GAR, Carvalho CJB, Casari AS, Constantino R (Eds) *Insetos do Brasil. Diversidade e Taxonomia*. Holos. Ribeirão Preto, 701–743.
- Chandler L, Barrigosi JAF, Diaz EBS (1985) The first definitive host record for *Leucospis cayennensis* Westwood (Hymenoptera: Leucospidae). *Revista Ceres* 32: 170–174.
- Cooperband MF, Wharton RA, Frankie GW, Vinson SB (1999) New host and distribution records for *Leucospis* (Hymenoptera: Leucospidae) associated primarily with nests of *Centris* (Hymenoptera: Anthophoridae) in the dry forests of Costa Rica. *Journal of Hymenoptera Research* 8: 153–164.
- Couto RM, Camillo E (2014) Deposições de óleo por fêmeas de *Centris analis* (Fabricius) (Hymenoptera: Apidae: Centridini) parasitadas por *Physocephala* spp. (Diptera: Conopidae). *EntomoBrasilis* 7: 81–85. <https://doi.org/10.12741/ebrasilis.v7i2.382>

- Couto RM, Camillo E (2007) Influência da temperatura na mortalidade de imaturos de *Centris* (*Heterocentris*) *analis* (Hymenoptera, Apidae, Centridini). Iheringia 97: 51–55. <https://doi.org/10.1590/S0073-47212007000100008>
- Dórea MC, Aguiar CML, Figueroa LER, Lima LCL, Santos FAR (2010) Residual pollen in nests of *Centris analis* (Hymenoptera, Apidae, Centridini) in an area of Caatinga vegetation from Brazil. Oecologia Australis: 14: 232–237. <https://doi.org/10.4257/oeco.2010.1401.13>
- Garófalo CA, Camillo E, Serrano JC (1989) Espécies de abelhas do gênero *Centris* (Hymenoptera, Anthophoridae) nidificando em ninhos armadilhas. Ciência Cultural 41: 799
- Gaglianone MC (2005) Nesting biology, seasonality, and flower hosts of *Epicharis nigrita* (Friese, 1900) (Hymenoptera: Apidae: Centridini), with a comparative analysis for the genus. Studies of Neotropical Fauna and Environment 40: 191–200. <https://doi.org/10.1080/01650520500250145>
- Gazola AL, Garófalo CA (2009) Trap-nesting bees (Hymenoptera: Apoidea) in forest fragments of the State of São Paulo, Brazil. Genetics and Molecular Research 8: 607–622. <https://doi.org/10.4238/vol8-2kerr016>
- Gazola AL, Garófalo CA (2003) Parasitic behavior of *Leucospis cayennensis* Westwood (Hymenoptera, Leucospidae) and rates of parasitism in populations of *Centris* (*Heterocentris*) *analis* (Fabricius 1804) (Hymenoptera: Apidae: Centridini). Journal of Kansas Entomological Society 76: 131–142.
- Gazola AL, Garófalo CA (2002) Comportamento dos inimigos naturais de *Centris* (*Heterocentris*) *analis* (Hymenoptera: Apidae). In Del Claro K (Ed.) Anais do II Simpósio de Ecologia Comportamental e de Interações. Uberlândia, Brasil: 0–17.
- Gibson JF, Skevington JH (2013) Phylogeny and taxonomic revision of all genera of Conopidae (Diptera) based on morphological data. Zoological Journal of Linnean Society, London: 167: 43–81. <https://doi.org/10.1111/j.1096-3642.2012.00873.x>
- Grissell EE, Cameron SA (2002) A new *Leucospis* Fabricius (Hymenoptera: Leucospidae), the first reported gregarious species. Journal of Hymenoptera Research 11: 271–278.
- Groulx AF, Forrest JRK (2018) Nesting aggregation as a predictor of brood parasitism in mason bees (*Osmia* spp.). Ecological Entomology 43: 182–191. <https://doi.org/10.1111/een.12484>
- Jesus MBV, Garófalo CA (2000) Nesting behaviour of *Centris* (*Heterocentris*) *analis* in south-eastern Brazil (Hymenoptera, Apidae, Centridini). Apidologie 31: 503–513. <https://doi.org/10.1051/apido:2000142>
- Kamke R, Zillikens A, Heinle S, Steiner J (2008) Natural enemies and life cycle of the orchid bee *Eufriesea smaragdina* (Hymenoptera: Apidae) reared from trap nests. Journal of the Kansas Entomological Society 82: 202–209. <https://doi.org/10.2317/JKES-703.26.1>
- Kimsey LS (2006) Chrysididae. In: Handson PE, Gauld ID Hymenoptera de la región Neotropical. The American Entomological Institute, Gainesville 77: 544–550.
- Lima AR, Dias PG (2018) The New World species of *Leucospis* Fabricius, 1775 (Hymenoptera, Chalcidoidea, Leucospidae): an update of Bouček's revision with description of two new species from Brazil. Zootaxa 4441: 1–45. <https://doi.org/10.11646/zootaxa.4441.1.1>
- Lucia M, Alvarez LJ, Abrahamovich AH (2013) First record of Melaloncha (Diptera: Phoridae) parasitoid associated with *Bombus* (Apidae: Bombini) in Argentina. Journal of Apicultural Research 52: 72–73. <https://doi.org/10.3896/IBRA.1.52.2.15>



- Lückmann J, Assmann T (2006) Reproductive biology and strategies of nine meloid beetles from Central Europa (Coleoptera: Meloidae). *Journal of Natural History* 39: 4101–4125. <https://doi.org/10.1080/00222930500533823>
- Magalhães CB, Freitas BM (2013) Introducing nests of the oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini) for pollination of acerola (*Malpighia emarginata*) increases yield. *Apidologie* 44: 234–239. <https://doi.org/10.1007/s13592-012-0175-4>
- Malfi RL, Roulston TAH (2014) Patterns of parasite infection in bumble bees (*Bombus* spp.) of Northern Virginia. *Ecological Entomology* 39: 17–29. <https://doi.org/10.1111/een.12069>
- Marston N (1970) Revision of New World species of *Anthrax* (Diptera: Bombyliidae), other than the *Anthrax albofasciatus* group. Smithsonian Institution Press, Washington, DC.: 1–149. <https://doi.org/10.5479/si.00810282.43>
- Martins AC, Luz DR, Melo GAR (2017) Palaeocene origin of the Neotropical lineage of cleptoparasitic bees Ericrocidini-Rhathymini (Hymenoptera, Apidae). *Systematic Entomology* 43: 510–521. <https://doi.org/10.1111/syen.12286>
- Melo GAR, Aguiar AP, Garcete-Barrett BR (2012) Hymenoptera. In: Rafael J, Melo GAR, Carvalho CJB, Casari AS, Constantino R (Eds) *Insetos do Brasil. Diversidade e Taxonomia*. Holos, Ribeirão Preto, 553–612.
- Melo GAR, Faria-Junior LRR, Marchi P, Carvalho CJB (2008) Small orchid bees are not safe: parasitism of two species of *Euglossa* (Hymenoptera: Apidae: Euglossina) by conopid flies (Diptera: Conopidae). *Revista Brasileira de Zoologia* 25: 573–575. <https://doi.org/10.1590/S0101-81752008000300028>
- Michener CD (2007) *The Bees of the World*. The John Hopkins University Press, Baltimore.
- Morato EF, Garcia MVB, Campos LAO (1999) Biologia de *Centris* Fabricius (Hymenoptera, Anthophoridae, Centridini) em matas contínuas e fragmentos na Amazônia Central. *Revista Brasileira de Zoologia* 16: 1213–1222. <https://doi.org/10.1590/S0101-81751999000400029>
- Morgan D (1984) Cuckoo-Wasps (Hymenoptera, Chrysididae). *Handbooks for the Identification of British Insects*. Vol. 6. Royal Entomological Society of London, London.
- Moure JS, Melo GAR (2012) Centridini Cockerell and Cockerell, 1901. In: Moure JS, Urban D, Melo GAR (Eds) *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – Online Version*. <http://moure.cria.org.br/index>
- Moure JS, Melo GAR, DalMolin A (2012) Megachilini Latreille, 1802. In: Moure JS, Urban D, Melo GAR (Eds) *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – Online Version*. <http://moure.cria.org.br/index>. [Accessed 20 October 2017]
- Moure-Oliveira D, Rocha-Filho LC, Ferreira-Caliman MJ, Garófalo CA (2017) Nesting dynamic and sex allocation of the oil-collecting bee *Centris (Heterocentris) analis* (Fabricius, 1804) (Apidae: Centridini), *Journal of Natural History*. <https://doi.org/10.1080/00222933.2017.1324052>
- Noyes JS (2017) Universal Chalcidoidea Database. World Wide Web electronic publication. <http://www.nhm.ac.uk/chalcidoids>. [Accessed 25 October 2018]
- Oliveira-Rebouças P, Aguiar CML, Ferreira VS, Sodré GS, Carvalho CAL, Gimenes M (2018) The cavity-nesting bee guild (Apoidea) in a Neotropical sandy coastal plain. *Sociobiology* 65: 706–713. <https://doi.org/10.13102/sociobiology.v65i4.3339>

- Oliveira OS, Gonçalves RB (2017) Trap-nesting bees and wasps (Hymenoptera, Aculeata) in a Semidecidual Seasonal Forest Fragment, Southern Brazil. *Papéis Avulsos de Zoologia* 57: 149–156. <https://doi.org/10.11606/0031-1049.2017.57.13>
- Oliveira R, Schlindwein C (2009) Searching for a manageable pollinator for acerola orchards: The solitary oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini). *Journal of Economic Entomology* 102: 265–273. <https://doi.org/10.1603/029.102.0136>
- Parker FD (1977) Biological notes on some Mexican bees (Hymenoptera: Megachilidae, Anthophoridae), *Pan-Pac Entomologist* 53: 189–192.
- Pärn M, Soon V, Vallisoo T, Hovi K, Luig J (2015) Host specificity of the tribe Chrysidini (Hymenoptera: Chrysididae) in Estonia ascertained with trap-nesting. *European Journal of Entomology* 112: 91–99. <https://doi.org/10.14411/eje.2015.012>
- Pereira M, Garófalo CA, Camillo E, Serrano, JC (1999) Nesting biology of *Centris* (*Hemisiella*) *vittata* Lepeletier in southeastern Brazil (Hymenoptera, Apidae, Centridini). *Apidologie* 30: 327–338. <https://doi.org/10.1051/apido:19990409>
- Rabelo LS, Vilhena AMGF, Bastos EMAF, Augusto SC (2014) Differentiated use of pollen sources by two sympatric species of oil-collecting bees (Hymenoptera: Apidae). *Journal of Natural History* 48: 25–26. <https://doi.org/10.1080/00222933.2014.886342>
- Rasmussen C, Cameron SA (2004) Conopid Fly (Diptera: Conopidae) Attacking Large Orchid Bees (Hymenoptera: Apidae: Eulaema). *Journal of Kansas Entomological Society* 77: 61–62. <https://doi.org/10.2317/0306.16.1>
- Rocha-Filho LC, Packer L (2015) Revision of the Neotropical subgenera *Coelioxys* (*Platycoelioxys*) Mitchell and *C. (Rhinocoelioxys)* Mitchell (Hymenoptera; Megachilidae) with the description of one new species. *Zootaxa* 3941: 151–203. <https://doi.org/10.11646/zootaxa.3941.2.1>
- Rocha-Filho LC (2015) A contribution to the taxonomy of the cleptoparasitic bee subgenus *Cyrtocoelioxys* Mitchell of *Coelioxys* Latreille (Hymenoptera: Megachilidae). *Annales Zoologici* 65: 687–703. <https://doi.org/10.3161/00034541ANZ2015.65.4.011>
- Rocha-Filho LC, Morato EF, Melo GAR (2009) New host records of *Aglaomelissa duckei* and compilation of host associations of Ericrocidini bees (Hymenoptera: Apidae). *Revista Brasileira de Zoologia* 26: 299–304. <https://doi.org/10.1590/S1984-46702009000200012>
- Rocha-Filho LC, Silva CI, Gaglianone MC, Augusto SC (2008) Nesting behavior and natural enemies of *Epicharis* (*Epicharis*) *bicolor* Smith (Hymenoptera: Apidae). *Tropical Zoology* 21: 227–242.
- Roubik DW (1989) Ecology and natural history of tropical bees, Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511574641>
- Rozen Jr JG, Melo GAR, Aguiar AJC, Alves-dos-Santos IA (2006) Nesting biologies and immature stages of the Tapinotaspidine bee genera *Monoeca* and *Lanthanomelissa* and of their Osirine Cleptoparasites *Protosiris* and *Parepeolus* (Hymenoptera: Apidae: Apinae). *American Museum Novitates* 3501: 1–60. [https://doi.org/10.1206/0003-0082\(2006\)501\[0001:NB AISO\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2006)501[0001:NB AISO]2.0.CO;2)
- Santos AM, Serrano JC, Couto RM, Rocha LSG, Mello-Patiu CA, Garófalo CA (2008) Conopid flies (Diptera: Conopidae) parasitizing *Centris* (*Heterocentris*) *analis* (Fabricius) (Hymenoptera: Apidae, Centridini). *Neotropical Entomology* 37: 606–608. <https://doi.org/10.1590/S1519-566X2008000500018>

- Scott VL, Kelley ST, Strickler K (2000) Reproductive biology of two *Coelioxys* cleptoparasites in relation to their *Megachile* hosts (Hymenoptera: Megachilidae). *Annales of Entomological Society of America* 93: 941–948. [https://doi.org/10.1603/0013-8746\(2000\)093\[0941:RBOTCC\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2000)093[0941:RBOTCC]2.0.CO;2)
- Soon V, Sarma U (2011) Mitochondrial phylogeny of the *Chrysis ignita* (Hymenoptera: Chrysididae) species group based on simultaneous Bayesian alignment and phylogeny reconstruction. *Molecular Phylogenetics and Evolution* 60: 13–20. <https://doi.org/10.1016/j.ympev.2011.04.005>
- Torretta JP, Molina GAR, Aquino DA (2017) Life cycles and host-parasitoid relationships of five species of *Leucospis* wasps in Argentina (Hymenoptera: Leucospidae). *Journal of Natural History*. <https://doi.org/10.1080/00222933.2017.1353151>
- Torretta JP (2015) Host-parasite relationships and life cycles of cuckoo wasps in agro-ecosystems in Argentina (Hymenoptera: Chrysididae: Chrysidini). *Journal of Natural History* 49:1641–1651. <https://doi.org/10.1080/00222933.2015.1005710>
- Tormos J, Asis JD, Gayubo SF, Mingo E (1996) Description of the mature larvae of *Chrysis gracillima* and *Omalus biaccinctus* and new data on the biology of *Trichrysis cyanea* (Hymenoptera: Chrysididae). *Florida Entomologist* 79: 56–63. <https://doi.org/10.2307/3495754>
- Vilhena AMGF, Rabelo LS, Bastos EMAF, Augusto SC (2012) Acerola pollinators in the savanna of Central Brazil: temporal variations in oil-collecting bee richness and a mutualistic network. *Apidologie* 43: 51–62. <https://doi.org/10.1007/s13592-011-0081-1>
- Vinson SB, Frankie GW, Willians HJ (1996) Chemical ecology of bees of the genus *Centris* (Hymenoptera: Apidae). *Florida Entomologist* 79: 109–129. <https://doi.org/10.2307/3495809>
- Vinson SB, Frankie G, Rao A (2011) Field behavior of parasitic *Coelioxys chichimeca* (Hymenoptera: Megachilidae) toward the host bee *Centris bicornuta* (Hymenoptera: Apidae). *Apidologie* 42: 117–127. <https://doi.org/10.1051/apido/2010041>
- Wcislo WT, Arneson L, Roesch K, Gonzalez V, Smith A, Fernández H (2004) The evolution of nocturnal behaviour in sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera: Halictidae): an escape from competitors and enemies? *Biological Journal of Linnean Society* 83: 377–387. <https://doi.org/10.1111/j.1095-8312.2004.00399.x>
- Wcislo WT, Cane JH (1996) Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Reviews of Entomology* 41: 257–286. <https://doi.org/10.1146/annurev.en.41.010196.001353>
- Yeates DK, Greathead D (1997) The evolutionary pattern of host use in the Bombyliidae (Diptera): a diverse family of parasitoid flies. *Biological Journal of Linnean Society* 60: 149–185. <https://doi.org/10.1111/j.1095-8312.1997.tb01490.x>